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LIFE HISTORY AND GENERAL BIONOMICS OF *TRIRHABDA SERICOTRACHYLA* BLAKE (COLEOPTERA: CHRYSOMELIDAE) IN SOUTHERN CALIFORNIA

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This study examines life history characteristics of *Trirhabda sericotrachyla* Blake[1] in relation to its host plant, *Artemisia californica* Less. (Asteraceae). The results of laboratory rearing studies were correlated with field observations made at several locations within 5 km of the University of California, Irvine, campus from 1977 to 1979. Host plant records for other sympatric *Trirhabda* spp. observed during the field phase of the study are also summarized.

Systematics and Host Plant Relationships

Other than the original description and host records (Blake, 1931; Hogue, 1970), biological information about *T. sericotrachyla* is lacking. The genus was introduced by LeConte (1865) and its systematics have been reviewed several times (Blake, 1931, 1951; Wilcox, 1965; Hogue, 1970). Thirty-seven species, including three fossil forms, comprise the genus which is distributed throughout North and Central America (Wilcox, 1971). According to field observations, analysis of host records, and rearings, Hogue (1970) concluded that species of *Trirhabda* were restricted to host plants in the Asteraceae and Hydrophyllaceae. The available literature recently reviewed by Hogue (1970) includes accounts of the life histories of *T. canadensis* (Kirby) (Balduf, 1929), *T. flavolimbata* (Mannerheim) (Tilden, 1953), *T. pilosa* (Blake) (Arnott, 1957; Pringle, 1960; Banham, 1961), and *T. nitidicollis* LeConte (Massey and Pierce, 1960). A description of the larva of *T. canadensis* and notes on several other species appeared in Boving (1929).

Four species of *Trirhabda* probably occur sympatrically in the San Joaquin Hills of Orange County, California, where they segregate according to differences in host plant preference and/or suitability. Three species, *T. sericotrachyla*, *T. luteocincta* LeConte, and *T. confusa* Blake, have previously been reported from this area (Hogue, 1970). *Trirhabda confusa* was not located during this study but the senior author observed another species, *T. geminata* Horn, on a previously unreported host, *Encelia californica* Nutt. (Asteraceae). Older specimens in the University of California, Irvine,

Museum of Systematic Biology confirm this finding. Previous host records (Blake, 1931; Hogue, 1970) indicate that *T. geminata* occurs on *E. farinosa* Gray and *E. virginensis* A. Nels. in both high and low elevation deserts of southern California.

On hillsides in the coastal sage scrub community near Irvine, California, *T. sericotrachyla, T. geminata,* and *T. luteocincta* can be found in close proximity. *Trirhabda luteocincta* occurs on *Haplopappus venetus* ssp. *vernonioides* (Nutt.) Hall and *H. palmeri* Gray (Asteraceae), which can be intertwined with *A. californica* branches supporting *T. sericotrachyla*. "*Aplopappus*" was recorded as a host for *T. luteocincta* (Blake, 1931), but Hogue (1970) did not locate it on any *Haplopappus* species and reported its host plant as *A. californica*. During the course of this study, we occasionally observed adult *T. luteocincta* on *A. californica* foliage, but could not find larvae or adults feeding on this plant. Attempts to switch first instar larvae of *T. luteocincta* from *H. palmeri* to *A. californica* were unsuccessful.

Trirhabda sericotrachyla is locally common in coastal sage scrub communities where it feeds exclusively on *A. californica* as both larvae and adults (Blake, 1931; Hogue, 1970) and is the plant's principal insect defoliator. With a few exceptions, the life history of *T. sericotrachyla* corresponds with that known for other species in the genus. The insect ranges along much of the coast of California and parts of Oregon and Washington (Hogue, 1970) where its distribution roughly coincides with that of *A. californica* (Munz and Keck, 1959). It is univoltine and can attain high densities which may cause severe defoliation of its host, a characteristic shared by other *Trirhabda* species (Hogue, 1970; F. Messina, pers. comm.).

Extensive stands of *A. californica* occur in undeveloped areas of cismontane southern California. The plant is a primary indicator of the coastal sage scrub community (Epling and Lewis, 1942; Kirkpatrick and Hutchinson, 1977) and is frequently the dominant shrub in this association (Mooney, 1975; Axelrod, 1978). It is a drought deciduous perennial that sheds its foliage in summer or fall depending on environmental conditions and flushes shortly after the first winter rains.

The Egg

During laboratory rearing studies oviposition behavior was observed on many occasions. Attempts to monitor oviposition in the field, however, were virtually unsuccessful because females deposit eggs only in stem crevices at soil level. Detailed examination of foliage and branches and screening of soil and duff near several colonized plants yielded no eggs. In the lab most eggs were laid in narrow crevices and folds of the rearing container or were hidden beneath pieces of toweling provided for cover.

The eggs are deposited in May or June and hatch after *A. californica*

Table 1. Proportions of *T. sericotrachyla* eggs hatching under different temperature and humidity conditions.

Humidity treatment	Temperature treatment		
	Lab conditions	Field conditions	Pre-cooled
Control	0.02	0.0	0.0
Wet–dry	0.02	0.0	0.12
Saturated	0.32	0.38	0.30

plants initiate new growth during the winter rainy season. They are laid in clusters of 15–50 eggs, several days apart. The individual eggs are 1–2 mm long with a sculptured chorion. When laid they are golden tan and slowly darken, and the clusters are enclosed in an adhesive matrix that quickly hardens.

Egg hatching.—Several experimental treatments were utilized to evaluate the effects of humidity and temperature on the timing of eclosion and hatching success. The galerucines, *Diabrotica virgifera virgifera* LeConte and *D. longicornis barbari* Smith and Lawrence, the western and northern corn rootworms, lay eggs that undergo winter-diapause (Chiang, 1973; Krysan et al., 1977). Their embryonic dormancy is influenced by humidity (Krysan et al., 1977), and the timing of eclosion is affected by temperature (George and Ortman, 1965). Both of these environmental factors are incorporated in rearing programs for corn rootworms (Branson et al., 1975).

The hatching experiment employed two different methods of humidifying the environment combined with three temperature treatments. The eggs were allowed to remain in bare petri dishes at normal laboratory conditions for about 150 days (approximately until the time of the first fall rains in the field) before the experiment was started. Two replicates for each treatment of approximately 60 eggs (laid over a three week span in May 1978) were placed on sterilized U.C. Mix potting soil in petri dishes. One moisturizing treatment consisted of maintaining the eggs in an environment of continuously high humidity by saturating the soil weekly and keeping the petri dish covered. Eggs in the second humidity treatment were also moistened weekly but were allowed to dry out between waterings. Temperature conditions were: (1) normal laboratory regime near a south facing window with light augmented by fluorescent room lights; (2) cooling in a refrigerator at 5°C for one month prior to exposure to the laboratory conditions mentioned above; and (3) maintaining the eggs outdoors under shelter where temperatures ranged from 1–30°C. Control (unmoistened) eggs were used with each temperature treatment. Emerging first instar larvae climbed to the petri dish lid and were easily counted.

The hatchability of eggs was markedly determined by humidity (Table 1),

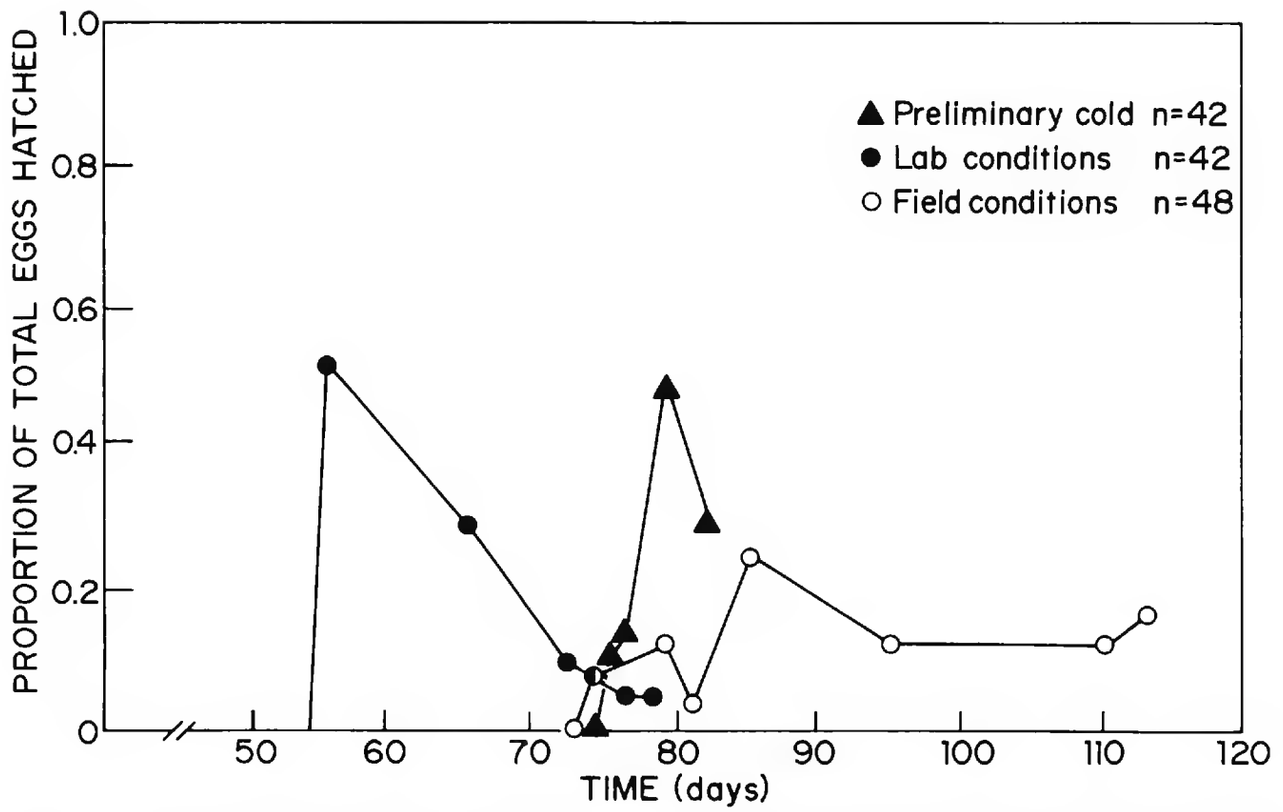

Fig. 1. Timing of eclosion of *T. sericotrachyla* eggs following initial exposure to saturated atmospheres and a, preliminary cooling at 5°C for 30 days, ▲; b, laboratory temperatures, 21° ± 2°C, ●; c, field conditions, 1°–30°C, ○.

with pronounced success only in chambers having saturated atmospheres. The timing of eclosion was largely influenced by temperature (Fig. 1). One month of chilling at 5°C resulted in a compressed hatch duration, while eggs maintained outdoors under a widely fluctuating temperature regime hatched over a prolonged period. Eggs exposed to the higher laboratory temperatures began hatching after 55 days, whereas eggs exposed to fluctuating outdoor temperatures did not achieve an equivalent cumulative percent hatch until 30 days later.

An abbreviated hatch duration is also seen with prechilled eggs of *D. virgifera* (George and Ortman, 1965). Krysan (1972) showed that the embryonic rudiment develops to the diapause stage either before or during chilling, which suppresses further development. Release from chill allows rapid development and relative synchrony. *Trirhabda sericotrachyla* may undergo a similar diapause, but hatch duration under field conditions lasts much longer than when eggs have been cooled in the lab. Prolonged winter chills are very uncommon in coastal southern California, and any synchronizing effects of low temperatures are probably negated by the combined influences of extended egg laying by adults in late spring, daily temperature fluctuations, and the possible sensitivity of the eggs to some stimulus correlated with the initiation of shoot elongation by the plant.

Hatching success under field conditions is unstudied. Corn rootworm rearing programs employ humidified environments throughout embryological development with hatching success approaching 100% (Branson et al., 1975). Coastal southern California receives very little rainfall from April to October, and despite the presence of interstitial water in the soil or condensation of atmospheric moisture at night, humidity in the microenvironment of field eggs would not be expected to remain near 100%. However, the lengthy and well protected egg stage effectively passes the dry summer and fall after the host foliage is shed. Embryonic diapause in *D. virgifera* is thought to have originated as an adaptation to similar environmental conditions in Mexico and secondarily functions to protect the eggs during harsh winters in temperate latitudes (Krysan et al., 1977; Branson et al., 1978).

Whether eggs remaining unhatched the first year will eclose at a future time remains untested. Hatchability of western corn rootworm eggs is reduced by 80% after one year's storage at 5°C (Branson et al., 1975). Several clusters of *T. sericotrachyla* eggs which were maintained under normal laboratory conditions for one year were desiccated and lacking protoplasm. Fungal contamination is difficult to avoid after several months in humidified chambers, and these organisms may also invade eggs under field conditions.

As with other stenophagic insects, *T. sericotrachyla* is closely adapted to the annual cycle of its host. At a time of year when few herbivorous insects are evident, and the physical environment can cause flooding or freeze damage to *A. californica,* new larvae emerge from the egg following early leaf development. The synchrony of insect developmental stages with the availability of the most suitable part of the plant is essential to successful exploitation by herbivores (Breedlove and Ehrlich, 1972; Kogan, 1975; Labeyrie, 1978). *Artemisia californica* plants are variable in their time of flushing, and *T. sericotrachyla* eggs appear to be correspondingly variable in their embryonic duration. The population must complete larval development, metamorphose, and attain reproductive maturity within a period of time that may be compressed from either end. With mild winters in southern California, *T. sericotrachyla* can afford to emerge early from the egg stage in most years in order to exploit the youngest foliage available.

The Larva

Monitoring of the field sites began in mid-January to detect the presence of first instar larvae on *A. californica* foliage. The sites were visited regularly at several day intervals thereafter as long as larvae or adults were present, and detailed observations of insect behavior were made frequently.

Newly eclosed first instar larvae collected from the field were fed in the lab on fresh host branches maintained in small jars of distilled water. A filter paper barrier was used to prevent the larvae from entering the water, and

Table 2. Mean duration ± SD, ranges of length and wet weight, and mean head capsule width ± SD of *T. sericotrachyla* larvae reared under laboratory conditions.

Larval instar	Length (mm)	Head capsule width (mm)	Wet weight (mg)	Duration (days)
1	1–3	0.5 ± 0.1, N = 12	0.8–3.0	6.5 ± 1.5, N = 40
2	3–7	0.8 ± 0.2, N = 15	2–8	6.4 ± 1.6, N = 38
3	7–13	1.2 ± 0.2, N = 15	7–74	6.5 ± 1.8, N = 38

the vial was placed in a plastic cottage cheese container to catch any larvae dropping from the filter paper. Larval food was changed, and each larva was weighed approximately every two days. Larvae could also be reared in petri dishes containing moistened filter paper. Laboratory conditions were a south facing window augmented by normal overhead fluorescent lighting while people were present, temperature 20–24°C, relative humidity 40–50%.

First instar larvae appeared in early February in the field with the time of emergence varying between sites and between years. Emergence lasted over a two month span and varied both between and within plants. Generally most of the larvae on a given plant emerged within a two to three week period, but a few first instar larvae could be found on a plant even after many of their predecessors had migrated to the soil to pupate.

First instar larvae were concentrated near the growing tips with 84% (N = 245) on the distal ¼ of new shoots. A substantial proportion (25%) was found within the terminal sheath of leaves at the shoot apex. The vast majority (91%) were on the upper surface of a leaf, but whether this is advantageous for early feeding or adhering to the leaf surface is unknown. Older larvae were more widely distributed over the foliage. They appeared to be more tolerant of mature foliage and could consequently disperse away from crowded shoot tips. New growth was sometimes destroyed during intense herbivory by the beetles, forcing larvae to seek food elsewhere.

Size ranges and the duration of the three larval instars are indicated in Table 2. Four larval instars were reported for *Trirhabda* by Hogue (1970), an unaccountable observation considering Boving's (1929) monograph on galerucine larvae and considerable work done on other insects of economic importance in the group. First instar larvae are mostly piceous in color with occasional hints of metallic luster, moderately pubescent, and highly mobile. The second instar larvae change to a metallic blue or green, typical of many galerucine larvae (Boving, 1929).

Ecdysis requires several hours and is preceded by a nonfeeding period of undetermined length. Cast larval head capsules and thoracic remnants were not restricted to the inner portions of the plant as Hogue (1970) reported

for the genus, but were found generally distributed about the foliage. Larvae in the third instar reared in the lab were quite sedentary until they concluded feeding prior to descending to the soil for pupation.

Before pupation, larvae would either climb downward or drop to the soil surface where they would soon begin burrowing to a depth of 1–2 cm. Under laboratory conditions larval development prior to entering the soil averaged 19 days (SD = 3, N = 40). By mid-May the vast majority of larvae had disappeared.

The quiescent pre-pupal period lasted several days during which up to half of the maximum larval weight was lost. The metallic color was retained until shortly before pupation when the insect darkened and the luster disappeared. Most, but not all, of the larvae created a spherical cell of soil particles bound by anal secretions, approximately 1 cm in diameter, in which pupation took place. The larva assumed a C-shaped form with its head up within a cell, or it rested on its side if no cell was constructed. These observations on pre-pupal larvae conform to those of Hogue (1970).

With respect to eight neighboring perennial shrubs (O'Brien, 1980), *T. sericotrachyla* larvae fed exclusively on *A. californica*. Host specificity experiments did not preclude potential conditioning influences as newly eclosed larvae obtained from the field already feeding on *A. californica* were used for the tests, but the results correlate with field observations and prior host records. Factors regulating host discrimination are untested, but could involve several types of secondary chemicals known from Asteraceae in general and *Artemisia* in particular. These components include monoterpenes (Halligan, 1975, 1976), sesquiterpene lactones (Mabry and Bohlman, 1977), flavenoids (Rodriguez et al., 1972), and coumarins (Shafizadeh and Melnikoff, 1970).

Larval migration.—The spring of 1978 was exceptionally wet in southern California, and virtually all *A. californica* plants at one field site were severely defoliated, presumably because of prolonged surface flooding and saturation of the root zone. Second and third instar larvae had dropped from their host plants and were actively crawling over the surface, in contrast to pre-pupal larvae which immediately burrow into the soil. The vast majority of these migrating larvae sustained mortality from desiccation and/or starvation while stranded in surface depressions from which they were unable to escape.

To determine if such disenfranchised larvae would seek new host plants, 100 vigorously mobile, third instar larvae were collected from the soil surface and marked with water soluble, non-toxic poster paint. They were released shortly thereafter in a slightly sloping but relatively flat area where a number of small (0.5 m tall) *A. californica* plants had not suffered appreciable damage. Many larvae were dropping at the time experimental insects were obtained, so most of the insects used had probably only recently de-

parted their host plants. The presence of marked larvae in surrounding plants and their distance traveled were recorded on several occasions during the following 24 hours.

This experiment established that the probability of successful colonization of a new host plant was low (7.0%) even with plant densities of 1.03/m^2. Only 4.0% of the larvae were consistently able to travel further than 2.0 m in 24 hours, although most of them made an initial attempt to move. Most larvae traveled downslope, but many were unable to avoid or climb out of surface irregularities. In the lab, a less severe habitat than the outdoor soil surface, second instar larvae died within 72 hours without food or moisture, which provides a crude estimate of the time available for migrating larvae to locate a new host.

The possibility that heavy feeding by *T. sericotrachyla* larvae aggravated the stress imposed on the plants by saturated soil could not be explored as all defoliated plants had been infested by insects. Of 36 defoliated plants which were being used to sample densities of beetle larvae in the field, 17 resprouted about 2 months later. Foliage on the other plants did not regenerate, and they were dead the following spring. *Artemisia californica* undergoes similar die-back and regeneration in response to prolonged exposure to freezing temperatures (Mooney, 1977). Defoliation in response to environmental stress of plants with the capacity for resprouting could confer an added benefit of reduced herbivory. We have observed heavy mortality in *T. geminata* populations on *Encelia farinosa* near Riverside, California, which suffered extensive freeze damage in January 1979, and resprouted several weeks later. Breedlove and Ehrlich (1972) postulated a similar mechanism for high altitude lupines to rid themselves of flower-feeding lycaenid butterflies. In the present case, the density of first instar *T. sericotrachyla* larvae the following year on plants that survived defoliation was about half that preceding leaf-drop.

The Pupa

Larvae were allowed to pupate in the bottom of plastic cups which contained about 2 cm of U.C. Mix potting soil and were placed in an emergence cage. Later experiments have shown that the addition of soil is unnecessary for successful pupation; the insects will simply pupate in the bottom of a bare petri dish to which a small piece of moistened filter paper is added.

At pupation the last larval cuticle splits longitudinally along the dorsum, revealing a typical exarate pupa, yellowish in color that darkens somewhat over time. Larvae not constructing a pupation cell of soil particles metamorphosed normally. Pupae observed in the field were concentrated within 40 cm of the base of a plant. Some of them occurred on the surface, but most were found approximately 1 cm deep. Several *Trirhabda* species pupate near a depth of 1 cm, but others either burrow deeper or metamorphose

in the duff on the soil surface (Hogue, 1970). The average time from descent to the soil to adult emergence in the lab was 13 days (SD = 2, N = 40).

The Adult

Adults appeared in the field in late April or early May. They are rather cryptically colored with dusty blue to green elytra marginally bordered with yellow. Females are significantly larger than males, and the sexes can be readily distinguished according to the shape of the posterior margin of the terminal abdominal sternite, a characteristic of the tribe Galerucini (Wilcox, 1965). In males this edge is deeply invaginate centrally while in females it is shallowly concave. The cumulative sex ratio in the field over a one month period following the appearance of the first adults approximated 1:1 (N = 260). Females were markedly more abundant than males during the first several days, and males gradually caught up over the remainder of the month.

In the lab, adults climbed up a nearby plant after emergence where they generally remained inconspicuous near its interior for several days while they fed prior to mating. Hogue (1970) reported a pre-feeding period of 1–2 days following emergence. When females were ready to mate in the field, they frequently assumed positions toward the distal ends of branches, and males approached them from below. Plants could occasionally be found with almost every terminal shoot supporting a female with very few males present. The female would frequently face downward, and as a male approached she would either wait for him to contact her or she would move downward to meet him before she turned around and allowed him to mount in a manner typical of the genus (Hogue, 1970). In *Diabrotica virgifera,* mating behavior is influenced by sex attractant pheromones (Ball and Chaudbury, 1973; Guss, 1976; Bartelt and Chiang, 1977; Lew and Ball, 1978). This possibility has not yet been explored for *Trirhabda* spp.

Upon emergence, one male and one female adult were placed in 2-quart ice cream cartons containing host branches maintained in water. Adult food was changed every two days, and filter paper barriers were used to block access to the water. Factors necessary for oviposition were unknown, so folded paper toweling, strips of paper toweling, and petri dishes containing U.C. Mix were placed in the bottom of the cartons to provide cover, tight crevices, and soil, respectively. The eggs were removed and counted every two days.

Copulation was observed to take much longer than the 1–3 minutes mentioned by Hogue (1970), occasionally lasting up to 15–20 minutes. The female caused the male to withdraw by starting to crawl and by wiggling her abdomen laterally until the male's position was no longer secure and he fell off. In the lab, polygamous matings also took place, which were usually separated by several days with a clutch of eggs deposited in the intervening period. However, in the presence of several males, a single female was

observed to accept at least two males in a four day period between depositing successive egg clusters. In addition, several females marked for identification mated with at least two different males in the field during observation periods a few days apart. Single matings are apparently the prevailing pattern for other *Trirhabda* spp. (Hogue, 1970). Although capable of mating several times, a female removed from the presence of males after she once mated continued to lay eggs throughout her adult life. The influence of multiple matings on fecundity is still unclear because of inadequate sample sizes. No information is available on the relative contribution of early and late sperm to the genetic constitution of these eggs.

Adult females lived up to 50 days in the lab during which time they deposited up to ten clusters totaling a maximum of 240 eggs. In general, females which lived longest and were largest at emergence laid the most eggs. However, there were enough exceptions to render statistically insignificant the slight positive correlations between fecundity and adult female size and longevity.

Adult dispersal.—Investigation of adult movement between plants in the field was accomplished by marking all the insects present on 8 plants at one field site with water soluble, non-toxic poster paint and recording their distribution every two or three days for the following month. Copulating pairs and females heavily laden with eggs were specially identified.

Of 312 marked insects, 15% were found on new hosts during the following 30 days. Males and females both disperse, although females have a tendency to remain longer with the same plant prior to mating than do males. The bulk of flight activity occurs in the afternoon while temperatures are elevated and breezes active. Most migrating insects move into or across the prevailing direction of the wind.

Over 80% of the insects observed to have migrated dispersed no further than 5.0 m from the plant where they were marked, with many moving only one or two plants away. The maximum distance covered by a marked insect (male) was about 60 m. The fate of lost marked insects is obviously uncertain, but based on observations of flying beetles, dispersal beyond 60 m is probable. However, the possibility of finding such insects was strongly reduced because of search time limitations. Several insects remained on a new plant for up to 2 weeks and two individuals, known to have migrated, returned to the plant where they were first identified.

Several gravid females were found on either the same (N = 3) or a different plant (N = 2) following a reduction in abdomen size, indicating that more than one clutch is possible under field conditions and that eggs are not necessarily deposited at the base of the same plant. One specially marked female was observed mating twice, and three males engaged in more than one copulation with different females. One male changed host plants 3 times and was observed mating twice on different hosts. Both males (N = 7) and

females (N = 6) which were not mating when marked did so later, and 2 of each sex copulated while on new host plants.

Natural Enemies

Trirhabda sericotrachyla has a complement of arthropod predators and parasitoids similar to that of other *Trirhabda* species (Hogue, 1970). *Lebia cyanipennis* Dejean, a diurnal arboreal carabid that specializes on leaf beetles (Madge, 1967), was infrequently observed searching *A. californica* foliage for prey, and occasionally captured one. A predaceous thrips, affixed to the dorsal surface just behind the head capsule of a third instar larva, fed on exudations seeping through the integument. The pentatomid, *Perillus splendidus* (Uhler), was more numerous than *L. cyanipennis,* and it fed on both larvae and adults. Other arthropod predators on adult *T. sericotrachyla* included orb-weaving and jumping spiders, and one unidentified assassin bug (Reduviidae).

Of several hundred third instar *T. sericotrachyla* larvae brought to the lab for experimental purposes, several that did not complete development assumed a barrel shape and eventually died. One individual yielded a single, unidentified tachinid fly. Nothing emerged from the other carcasses. Several presumably parasitized larvae were dissected, and parasite larvae (probably tachinids) were found in two hosts. The tachinid, *Aplomiopsis xylota* (Curran), caused substantial mortality among several *Trirhabda* species examined by Hogue (1970).

When disturbed, first and second instar larvae elevated and waved their abdomen in an apparent defensive reaction. Several *Trirhabda* species displayed this behavior in the presence of a tachinid parasitoid (Hogue, 1970). Other chrysomelid larvae are known to possess defensive glands which emit noxious substances (Blum et al., 1972; Blum et al., 1978), but these are presumed absent in the Galerucinae (Boving, 1929).

In the field several *T. sericotrachyla* larvae had suffered wounds from which extruded a hardened mass of fluid. Similar damage was caused when high densities of active larvae were kept in small containers in the lab. Whether the field condition resulted from intraspecific aggression or unsuccessful predator attacks is unknown.

Vertebrate predation was not observed except for a single black phoebe that was hawking airborne adult beetles in 1978. Although flocks of foliage gleaning birds (bushtits, warblers, gnatcatchers) are active in the coastal sage scrub habitat, birds do not appear to concentrate on the larvae, even though they occur in high densities and are quite visible. Predation by lizards was not observed, however, they have taken adult *Trirhabda* during laboratory feeding studies (Hogue, 1970). The possibility that *T. sericotrachyla* larvae sequester noxious components from their hosts or produce deterrent substances themselves has not been investigated.

No parasitoids emerged from several egg masses or 25 pupae taken to the lab for observation. None were previously reported by Hogue (1970). Shrews and insect eating rodents should be considered potential predators of the pupae, although no such activity was observed.

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Footnote

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